

- Observations and Remote Sensing*. <http://dx.doi.org/10.1109/JSTARS.2013.2265255>.
- Pack, R. T., Brooks, V., Young, J., Vilaca, N., Vatslid, S., Rindle, P., Kurz, S., Parrish, C. E., Craig, R., and Smith, P. W., 2012. An overview of ALS technology. In Renslow, M. S. (ed.), *Manual of Airborne Topographic Lidar*. Bethesda: ASPRS Press.
- Sithole, G., and Vosselman, G., 2004. Experimental comparison of filter algorithms for bare-Earth extraction from airborne laser scanning point clouds. *ISPRS Journal of Photogrammetry and Remote Sensing*, **59**, 85–101.
- Shan, J., and Toth, C., 2009. *Topographic Laser Ranging and Scanning: Principles and Processes*. Boca Raton: CRC Press.
- Slatton, K. C., Carter, W. E., Shrestha, R. L., and Dietrich, W., 2007. Airborne laser swath mapping: achieving the resolution and accuracy required for geosurficial research. *Geophysical Research Letters*, **34**, 1–5.
- Wehr, A., and Lohr, U., 1999. Airborne laser scanning—an introduction and overview. *Journal of Photogrammetry and Remote Sensing*, **54**, 68–82.

Cross-references

Light Detection and Ranging (LIDAR)

ALGAL BLOOMS

Patricia M. Glibert
Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, MD, USA

Synonyms

Harmful algal blooms; Nuisance algal blooms; Phytoplankton blooms; Red tides; Spring blooms

Definition

Algal blooms refer to the increase in biomass of algae due to increased growth or due to physical aggregation, leading to an above-normal accumulation and generally adverse ecosystem effects.

Introduction

Algae are a normal part of the aquatic ecosystem; they form the base of the aquatic food web. Of this large and diverse group of organisms, most are microscopic in size, but some are macroscopic. The microscopic algae are most often single cells, but some can form chains or colonies. Most microalgae live in the water column, while others live in or near to the sediment or attached to surfaces for some or all of their life cycle. Macroalgae can be multicellular and complex, the largest of which are the seaweeds.

Algal blooms are an important and natural component of the production of all aquatic systems, but especially those of temperate, subpolar, and coastal waters. Spring blooms are triggered by seasonal warming, increased light availability, water column stratification, and increased nutrient availability from riverine runoff or other sources. These blooms are important for

energy and material transport through the food web, and they also play an important role in the vertical flux of material out of the surface waters. These blooms are distinguished from those that are deemed “harmful.” Algae form harmful algal blooms, or HABs, when either they accumulate in massive amounts that alone cause harm to the ecosystem or the composition of the algal community shifts to species that make compounds (including toxins) that disrupt the normal food web or to species that can harm human consumers (Glibert and Pitcher, 2001). HABs are a broad and pervasive problem, affecting estuaries, coasts, and freshwaters throughout the world, with effects on ecosystems and human health, and on economies, when these events occur. This entry focuses on those algal blooms that are HABs. After an introduction to types of HABs and their effects, an emphasis is placed on the ecology and dynamics of the planktonic HABs, their global expansion, and approaches to their prediction and control.

Types of HABs (representative species groups and their effects)

Terminology

The term HAB is an operational one, not a technical one due the diversity of HAB types and effects. Due to the complexity of toxic or ecosystem effects, with the exception of a few species, there are no formal definitions of the concentrations of cells that determine a “bloom.” Many HAB events were formerly referred to as “red tides” because of their pigmentation, but this terminology has been supplanted because not all HABs are red; some may be green, yellow, or brown depending on their specific pigmentation.

While colors are used less frequently to distinguish different types of HABs, toxic properties are gaining favor as a way of distinguishing different types of HABs. By definition, all HABs cause harm, either to ecological, economic, or human health. *Toxic* HABs are those that involve toxins or harmful metabolites, such as toxins linked to wildlife death or human seafood poisonings, as described in more detail below. Of the tens of thousands of algal species, only a few percent have been documented to be toxic, although new toxins are being identified regularly (Landsberg, 2002). Some algal toxins are extremely potent, and thus toxic HABs can occur at cell densities that would not normally be taken to be in “bloom” proportion; they can, for example, sometimes cause poisonings at concentrations as low as a few hundred cells per liter.

Nuisance algal blooms, or NABs, do not produce toxins (or such toxins have not yet been identified), but are able to cause harm through the development of high biomass, leading to foams or scums, the depletion of oxygen as blooms decay, or the destruction of habitat for fish or shellfish such as by shading of submersed vegetation. Another distinction that some investigators have found useful is the group of HAB species that are not necessarily

toxic but do cause disruption to the grazer community and thus to trophic transfer and the food web in general. Such blooms have been coined *ecosystem disruptive algal blooms*, EDABs (Sunda et al., 2006).

Adding to the confusing terminology associated with HABs, some HABs are technically not “algae” at all, but rather small animal-like microbes that obtain their nutrition by grazing on other small algae or bacteria; they either do not photosynthesize at all or only do so in conjunction with grazing. These complex and diverse nutritional strategies are described in more detail below. Other “HABs” are more bacteria-like. These are the cyanobacteria (CyanoHABs), some of which have the ability to “fix” nitrogen from the atmosphere as their nitrogen source. All of these complexities underscore that the term “HAB” is simply an operational term, recognizing the group of species (not all of which are strictly algae) that can cause harm – to health, to the environment, or to the economy.

Common species groups and harmful properties

Of the thousands of species of marine phytoplankton from hundreds of genera, only a few can be highlighted here. Diatoms are the most common organisms associated with “spring blooms.” Diatoms are capable of rapid growth rates. They have a silicate shell and thus have a unique requirement for this element among the algae. Most diatoms are not harmful, but large spring blooms are associated with hypoxia or “dead zones” when the biomass sinks to deeper waters where it decomposes in oxygen-consuming processes. The annual development of summer hypoxia in Chesapeake Bay, for example, is due to these large spring bloom events (Kemp et al., 2005).

Diatoms may also be toxic, as is the case of *Pseudo-nitzschia* spp. that produce *domoic acid* that is responsible for the human illness called *amnesic shellfish poisoning* (Trainer et al., 2012). Exposure to this HAB group is now being linked to seizure and memory loss in laboratory animals and to premature births and strandings in animals such as sea lions (Johnson et al., 2010; Bargu et al., 2012).

Dinoflagellates are among the more common toxic HABs as well as NABs. Dinoflagellates all possess two dissimilar flagella; they often display complex life cycles and typically have much slower growth rates than diatoms. Many produce toxins that can kill fish directly or that intoxicate seafood with toxins that can be passed onto human consumers. One toxic dinoflagellate that causes significant human health effects is *Karenia brevis*, which produces large blooms along the coast of the Gulf of Mexico. This species produces a neurotoxin, brevetoxin, that is responsible for the human illness called *neurotoxic shellfish poisoning* (Backer and McGillicuddy, 2006). Several dinoflagellate species, including *Alexandrium* spp. and *Pyrodinium bahamense* (var. *compressum*), produce saxitoxin, responsible for *Paralytic Shellfish Poisoning* (PSP) (Backer and McGillicuddy, 2006). PSP has

been particularly problematic in Southeast Asia, where many human fatalities have been reported over the past several decades (Azanza and Taylor, 2001). Another example of a toxigenic dinoflagellate is *Karlodinium veneticum*. This species has been implicated in fish-kill events in the Chesapeake Bay area (Adolf et al., 2008) as well as in coastal waters of Southwest Africa, Europe, United States, Western Australia, and other temperate coastal environments.

Many HAB dinoflagellates develop large-scale blooms but do not produce toxins that have significant human effects. *Prorocentrum minimum* is one such globally distributed species. This species can produce high biomass blooms that affect the food web by altering ingestion rates and/or growth rates of consumers especially at the larval stages (Heil et al., 2005; Glibert et al., 2008). Benthic species of this genus are known toxin producers, however (Glibert et al., 2012).

Another significant group of HABs is the prymnesiophytes. Many, if not most, *Prymnesium* species are toxic to gill-breathing organisms and thus are responsible for many fish kills around the world, especially in eutrophic waters. For example, *Chrysochromulina polylepis* has been the cause of fish kills along the Norwegian coast, and *Prymnesium parvum* (Carter) is responsible for reoccurring fish kills in coastal and inland waters worldwide (reviewed by Edvardsen and Paasche, 1998; Edvardsen and Imai, 2006; Roelke et al., 2007). Along the North Sea coast, blooms of *Phaeocystis* spp. are common. Because they are mucilage rich, water can turn viscous, and beaches can be drenched in foam from decaying blooms (Lancelot, 1995).

The raphidophytes are yet another common HAB group distributed worldwide. These organisms have often caused large-scale fish mortalities, both in aquaculture settings and in natural environments. Among the more common HAB raphidophytes are *Heterosigma akashiwo* and *Chattonella* spp. The fish-killing properties of these species are due to their production of neurotoxins or to their production of reactive oxygen or other hemolytic agents (Edvardsen and Imai, 2006).

The CyanoHABs are increasingly an important nuisance and toxic HAB group affecting both freshwaters and estuarine and coastal systems worldwide. The most common toxins associated with this group of HABs are hepatotoxins, such as microcystin, nodularin, and cylindrospermopsin, but some species may also produce neurotoxins, such as anatoxin and saxitoxin (O’Neil et al., 2012). The world’s largest estuary, the Baltic Sea, is now annually affected by massive CyanoHAB blooms, including species such as *Nodularia*, *Anabaena*, and *Aphanizomenon*. One of the most common HAB types in freshwater as well as in upper estuaries and one exemplifying the effect of both direct and indirect contact is *Microcystis* spp. Exposure to water with this HAB or its toxin can cause skin irritation or respiratory irritation, but prolonged, repeated, or intensive exposure to the HAB toxin has been associated with tumor promotion,

especially liver cancer (Backer and McGillicuddy, 2006). As this toxin and other related toxins can affect the nervous system, there has been a suggestion that some neurological diseases such as Parkinson's disease or dementia may also be related to some of the toxic and bioreactive compounds originating from this HAB group (Ibelings and Chorus, 2007). Among the CyanoHAB group are also some species that attach to seagrass, corals, or sediment, such as *Lyngbya* which is also capable of producing a wide array of toxic or potentially toxic compounds, including Lyngbyatoxin and saxitoxin.

Although this entry is focused on planktonic HABs, for the sake of completeness, it is important to mention macroalgal HABs. Macroalgae also dominate the flora of many shallow estuaries, lagoons, and upper embayments, coral reefs, and rocky intertidal/subtidal habitats especially in polluted environments. A well-documented example of such a bloom occurred in 2008, when the macroalgal species *Enteromorpha prolifera* (also called *Ulva prolifera* or sea lettuce) occurred at the venue of the Olympic Games sailing competition, almost blanketing the water with filamentous scum (Hu et al., 2010). Blooms of this magnitude in this region had not previously been observed but have since reoccurred on a near annual basis associated with expanding aquaculture industries and eutrophication. It has been estimated that the cost associated with the management of the *E. prolifera* event in 2008 was greater than \$100 million.

Ecology and dynamics of HABs

For decades, HABs have been studied in all areas of the globe, but there is still much that is not well understood regarding the underlying processes behind the development or outbreak of species or species groups. In the simplest terms, the success of HABs lies at the intersection of their physiological adaptations of the HABs, the environmental conditions, interaction with co-occurring organisms, and physical dynamics of the water body.

Physiological adaptations

In order to grow and make new biomass, algae need to have the necessary materials and energy to make new biomass. The classic paradigm of algal blooms is that of microscopic "plants" or primary producers, dependent on light and the uptake of dissolved nutrients. However, as noted above, many HABs (the diatoms being the primary exception) may both engage in photosynthesis but may also graze on particles, including bacteria, cyanobacteria, other algae, or even bits of fish tissue. This complex nutrition or *mixotrophy* (the mix of different modes of nutrition) imparts advantages to organisms under conditions of low light (when photosynthesis would be reduced), under low nutrients (when inorganic nutrient uptake may be limited), or under conditions of imbalanced nutrient supply. Some species only use mixotrophy as a supplement, while others rely exclusively or nearly so on mixotrophic nutrition (Burkholder et al., 2008).

Some of these "algae" in fact do not make their own chlorophyll at all, but rather borrow their chloroplasts from the food they eat, a process termed *kleptochloroplasty*. Most all the major groups of eukaryotic phytoplankton, including most HABs, engage in mixotrophy to some extent (Flynn et al., 2013). Importantly, when an organism undertakes primary production (photosynthesis) and grazing, the two processes provide "more than the sum of the parts" in terms of benefits to the organisms (Mitra and Flynn, 2010), and thus these modes of nutrition have important consequences for understanding HAB success and in modeling the flow of energy and materials in microbial food webs (Flynn et al., 2013).

In addition to the complex nutrition of mixotrophy, the development of specific algal species may be a function of availability of specific nutrient forms. Using sources of nutrients not available to competitors may impart an advantage for certain species or species groups (Glibert and Burkholder, 2011). Many HABs have the ability to utilize organic forms of nitrogen and phosphorus, but mechanisms may vary. Some species have species enzymes for transport or metabolism of certain forms of organic nitrogen or phosphorus, while other species have the capability for the breakdown of organic compounds at the cell surface (Glibert and Legrand, 2006). Yet other species appear to be stimulated when complex organic molecules are provided in conjunction with inorganic nutrients. For example, in mesocosm experiments, Granéli et al. (1985) showed that dinoflagellate populations, including *Prorocentrum minimum*, were stimulated by inorganic nitrogen only when added in combination with humic acids.

Furthermore, the mechanisms for nutrient acquisition and the extent of dependence by a HAB on mixotrophy or on specific dissolved nutrient forms depend not only on the species, but also prevailing environmental factors such as temperature or light (Glibert and Burkholder, 2006). Thus, a given suite of nutrients may have different impacts in different sites and at different times. Smayda (2002) has suggested that different HAB dinoflagellates can be classified into a matrix, based on preferences organized by a nearshore/offshore gradient in decreasing nutrients, reduced mixing, and increasing light. In this matrix, estuarine species are defined as the dinoflagellates that are better adapted to low-light high-nutrient waters, but oceanic species are better adapted to high-light low-nutrient waters.

Many algae, including HABs, also have complex life cycles and behaviors that have important implications for their occurrence, distribution, and dynamics. Among life cycle stages for some algae are benthic cysts or other resting stages that give cells capability to withstand hostile or unfavorable environmental conditions. The metabolic switch from resting stages to motile stages often occurs for a population at or around the same time, allowing actively dividing cells to initiate a bloom. These cysts or spores provide a recurrent seed source or inoculum for planktonic populations, and this characteristic may be a critical factor in determining not only the geographic distribution of species but also their eventual abundance.

Some species form colonial stages during parts of their life cycle that have implications for grazers or may deter or protect species from viral or bacterial infection (Lancelot et al., 2002). Many HAB species are motile, and under certain environmental conditions, their swimming behavior or buoyancy may result in the formation of high-density patches (e.g., Franks, 1992; Kamykowski et al., 1998). Some cyanobacterial species are able to regulate their vertical positioning by synthesis and collapse of gas vesicles. Vertical movement by cells in a stratified environment may help to maximize encounter frequencies for sexual reproduction, minimize grazing losses, and allow cells to obtain nutrients at depth and light at the surface. All of these behaviors have important implications for species and bloom success and serve to underscore the deep complexity of the biology of these seemingly “simple” organisms.

Trophic interactions

The proliferation of HABs reflects the metabolism and specific growth of the “algal” cells, but also the dynamics of the species that are co-occurring with the HAB. It has long been argued that production of allelopathic exudates allows some harmful species to outcompete co-occurring phytoplankton (e.g., Granéli and Johansson, 2003). The ability of a HAB species to build their population under specific conditions is therefore related to the availability of sufficient nutrients to sustain it and to reduction in mortality rates. The response of zooplankton and other grazers to toxic algae is often species specific in terms of behavioral responses and toxin susceptibility. Many HAB species produce more toxins under stress, thereby allowing them to avoid predation and competition by killing their predators and the competing algal species (Granéli and Johansson, 2003). Fish and zooplankton avoid dense concentrations of certain HAB species, and some toxic species are rejected by predators or grazers. Grazing control of HABs can also depend on the population density of the harmful algae, as demonstrated for the brown tides in Narragansett Bay, USA, where suppression of grazing occurs above a threshold concentration (Tracey, 1988). A threshold effect may also occur if the daily production of new harmful cells becomes large enough to saturate the ingestion response of the grazers and the ability of grazers to increase their populations. In that case, population growth can accelerate dramatically (Donaghay, 1988).

Bacteria play an important role in controlling many HABs and regulating their impacts, including their toxicity. Bacteria may also interact with HABs in a positive manner by stimulating their growth. CyanoHABs, in particular, establish mutually beneficial consortia of microorganisms (Paerl and Millie, 1996). A different type of bacterial interaction with HAB species was described by Bates et al. (1995) who showed that the toxicity of the diatom *Pseudo-nitzschia* was dramatically enhanced by the presence of bacteria in laboratory cultures.

Likewise, viruses are also now known to have significant impacts on the dynamics of marine communities, and some have been found to infect algae and have been implicated in the demise of red or brown tide blooms (Fuhrman and Suttle, 1993). The extent to which any of the above interactions occur in natural waters and affect HAB dynamics is not well known and represents an important line of inquiry.

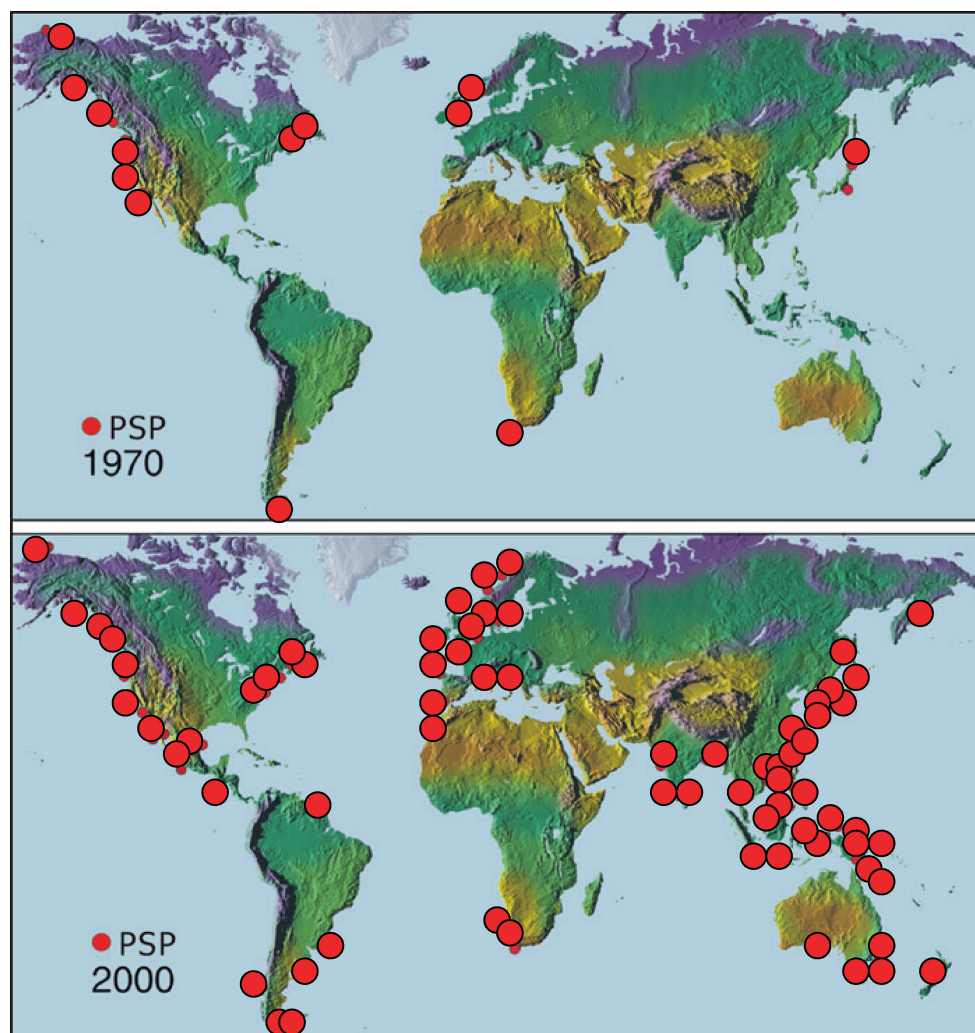
Physical dynamics

The physical environment is also intrinsically intertwined with the biology and ecology of algae. Many large-scale features have direct relevance to HABs or their likelihood for formation, including such features as tidal fronts, coastal jets, and upwelling. Some HABs tend to aggregate subsurface in thin layers. For example, in the Baltic Sea, the heterotrophic dinoflagellate *Dinophysis* may only be found in a 1–2 m layer, but at a depth of 20–25 m (Gisselson et al., 2002). As another example, it has been found off the coast of France that some subsurface layers are comprised of up to 100 % dinoflagellates, most of which are harmful and all of which are mixotrophic, a so-called magic carpet of toxic HABs (Gentien et al., 2008 and references therein). Stratification and mixing have pronounced effects on the distribution and success of HABs. Turbulence, also, has significant consequences for the growth and decline of HABs through its influence on the transport of nutrients, the mixing of phytoplankton through gradients of light, and even through direct impairment of growth. Many questions remain about the specific adaptations of cells to these local environments and the interplay between physics and biology in maintaining these microstructures.

Global expansion of algal blooms, HABs, and their effects

Both toxic and nuisance HABs are increasing throughout much of the world. For example, global occurrences of PSP increased dramatically over the three-decade period from 1970–2000 (Figure 1, Glibert et al., 2005a). Dead zones, another effect of high biomass algal blooms, are also increasing worldwide. The number of dead zones from excessive algal production has doubled each decade since the 1960s. Some systems have shown a progression from episodic to seasonal hypoxia and then, with increased nutrient enrichment, to more and more sustained hypoxia. Dead zones are now found in waters across the globe (Diaz and Rosenberg, 2008).

Although some of the factors contributing to the global expansion are natural, such as biological species dispersal, many others are considered to be a result of human activities, among which nutrient pollution is the most important. The exploitation of natural fish stocks has also, in some cases, led to a decrease in the control of HAB species by removal of the primary grazers through trophic cascade effects. Global climate change may also be important in the increase in HABs.



Algal Blooms, Figure 1 The global expansion of paralytic shellfish poisoning (PSP), one of the many harmful syndromes caused by harmful algal blooms (Figure reproduced from Glibert et al. (2005a) with permission of the Oceanography Society).

Links to eutrophication and altered nutrient stoichiometry

Overenrichment of coastal waters by nutrients is considered a major pollution problem worldwide (Howarth, 2008) and one of the most important factors contributing to global HAB increases (Anderson et al., 2002; Glibert et al., 2005b; Glibert and Burkholder, 2006; Heisler et al., 2008). Nutrient pollution is on the rise because of dramatic increases in human populations in many regions and concomitant increasing demands for energy, increases in nitrogen (N) and phosphorus (P) fertilizer use for agriculture, changes in diet that are leading to more meat production and animal waste, and expanding aquaculture industries (e.g., Howarth, 2008; Glibert et al., 2010; Bouwman et al., 2011; Bouwman et al., 2013). These industries have altered ecosystems through input of feed and feces, only a small percentage of which is incorporated in food biomass.

Increases in total nutrient load can support higher HAB biomass, and alterations in nutrient form can lead to a nutrient regime favoring HAB growth relative to other algal species. At the simplest level, harmful phytoplankton may increase in abundance due to nutrient enrichment, but remain in the same relative fraction of the total phytoplankton biomass. Even though non-HAB species are stimulated proportionately, a modest increase in the abundance of a HAB species can promote noticeable differences in the ecosystem because of its harmful or toxic effects. More frequently, a species or group of species dominates in response to nutrient enrichment or a change in the ratios of nutrient enrichment (Anderson et al., 2002).

The number of examples of algal blooms linked to eutrophication globally is long, and only a few are highlighted here. A species now well documented to be

associated with nutrient enrichment is the dinoflagellate *Prorocentrum minimum*. Globally, it is found in regions of the world where the coasts are receiving elevated nutrients from anthropogenic sources (Glibert et al., 2008). In the Chesapeake Bay, blooms of this species now appear to be 10- to 100-fold higher in maximum density than blooms recorded a few decades ago, and these increases track the nutrient load to the bay over the past several decades (Heil et al., 2005). In Puget Sound, Washington, a striking correlation has been found between the growth in documented cases of PSP over four decades and the growth in human population, based on US census statistics, strongly indicative of nutrient loading and eutrophication as the causative agent of change (Trainer et al., 2003). Based on analyses of frustules preserved in cores, blooms of the diatom *Pseudo-nitzschia* spp. in the Gulf of Mexico were also rare prior to the 1950s, but have increased significantly in abundance and frequency since then as nutrient loads from the Mississippi River have risen (Parsons et al., 2002). The Baltic Sea, the Aegean Sea, the Northern Adriatic, and the Black Seas have all experienced increases in HABs coincident with increases in nutrient loading (Granéli et al., 1999; Heil et al., 2005). In Northern European waters, blooms of the mucus-forming HAB species *Phaeocystis globosa* have been shown to be directly related to the excess nitrate content of riverine and coastal waters, that is, the nitrate remaining after other species of algae deplete silicate (Lancelot, 1995). One region where expansion of eutrophication-related HABs has been particularly pronounced has been along the Asian coast, where blooms have expanded in recent years in areal extent (from square kilometers to tens of square kilometers), in duration (days to months), in species, and in harmful impacts (Furuya et al., 2010). These increases all parallel the increase in the use of anthropogenic fertilizers and the accelerated development of China.

On shorter time scales, there are also examples of HABs responding rapidly to injections of nutrients from pulsed events. Beman et al. (2005) reported, during a 5-year study, a strong positive relationship between nitrogen-rich agricultural runoff to the Gulf of California and the development, within days, of extensive phytoplankton blooms. Similarly, *Pseudo-nitzschia pseudodelicatissima* was found a week after elevated ammonium levels were reported in these waters (Trainer et al., 2007), and in Chesapeake Bay, blooms of *Prorocentrum minimum* have been found to follow within days of elevated levels of urea following agricultural applications (Glibert et al., 2001).

Another important consideration in nutrient effects is the relatively recent phenomenon of changing stoichiometry of nutrient supplies. In many parts of the developed world, phosphorus reductions have been undertaken as a means to reduce or control algal blooms (e.g., in sewage effluents and laundry detergents), whereas nitrogen loads often are allowed to remain elevated. Thus, not only have many systems undergone eutrophication, but many

are showing signs of reversal due to this single nutrient reduction. The consequence is that many receiving waters are now not only enriched with nutrients, but these nutrients are in proportions that differ from those of decades past – and also diverge considerably from those that have long been associated with phytoplankton growth (Glibert and Burkholder, 2011). Many types of harmful algae appear to be able to thrive when nutrient loads are not in classically defined ideal proportions. Not only are many HABs able to access nutrients not available to competitors through mixotrophy, some species increase toxin production when growing in a state of nutrient imbalance. As examples, toxin production by the flagellates *Prymnesium parvum* and *Chrysochromulina polylepis* increases under both P and N stress, relative to toxin production in more nutrient-balanced growth conditions (Granéli and Flynn, 2006). As another example, in the dinoflagellate *Alexandrium tamarense*, the production of saxitoxin has been shown to increase by three to fourfold under phosphorus deficiency (Granéli and Flynn, 2006).

Adding to the complexity of nutrient effects, in some cases anthropogenic nutrients may not directly stimulate HABs, but may become linked to their growth and abundance following biogeochemical processing or following the stimulation of other components of the food web on which they may depend, or anthropogenic nutrients may be displaced in time and space leading to blooms that are displaced from their nutrient sources. It has recently been found, for example, that *Noctiluca*, the species responsible for classic “red” water, may well be a coastal or offshore manifestation of eutrophication, a mixotroph responding to successional planktonic changes in nutrient availability (Harrison et al., 2011). Relatedly, regulation of single nutrients (e.g., controlling phosphorus without controlling nitrogen) may lead to a situation where an estuary or inshore coastal environment is effectively phosphorus limited and blooms are controlled, but the nitrogen is displaced downstream where it eventually may help to support offshore blooms. Such effects have been documented for the Neuse River Estuary, the mid-region of the Chesapeake Bay, and the southern Baltic Sea region; all of these regions have experienced either episodic or sustained reductions in inshore blooms, but parallel increases in offshore blooms (Glibert et al., 2011 and references therein).

Links to climate

Climate ultimately controls the fundamental parameters regulating algal growth, including water temperature, nutrients, and light, and thus can be expected to result in changes in the species composition, trophic structure, and function of marine ecosystems. Examples can be found through the US and European coasts, where correlations between shifts in HAB species and the timing of their outbreaks and increases in mean water temperature have been documented. In addition, changing greenhouse gases, pH, as well as temperature are related to changes

in stratification, vertical exchange, upwelling, precipitation, and related trends, all of which can also influence the habitat for particular HABs (Moore et al., 2008). Moreover, some HABs, especially CyanoHABs, such as *Microcystis* spp., may become more toxic under higher temperatures (Davis et al., 2009).

Climate change may influence HAB expansion, and therefore, the frequency of some blooms may reflect the major changes in ecosystem structure that occur in response to interannual oscillations, such as those related to the El Niño Southern Oscillation (ENSO), or longer term cycles, such as North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO). In the northern Iberian Peninsula, for example, the abundance of the harmful dinoflagellate *Gymnodinium catenatum* was high during the mid-1980s when there was a transition from downwelling-favorable conditions to upwelling-favorable conditions following a shift in the NAO index (Alvarez-Salgado et al., 2003). In California, there is circumstantial evidence that a massive domoic acid event in Monterey Bay in 1998 was triggered by post-El Niño runoff (Scholin et al., 2000).

Estuaries: notable examples of sustained HABs in retentive habitats

Estuaries throughout much of the world are sites of frequent HABs (of all forms, including toxic, nuisance, and ecosystem disruptive). Estuaries – whether they be classic river-dominated systems, fjords, coastal embayments, or rias – have many unique features that may be promotive of HABs. Many estuaries are experiencing increasing nutrient loading from pressures of increasing population and housing developments, intensive agriculture in the watershed, and increased aquaculture production. Estuaries may receive considerable riverine input or may be highly retentive with minimal freshwater input or oceanic exchange. The comparatively shallow nature of estuaries (compared to open coasts and offshore regions) means that benthic processes as well as water column processes may be important in providing nutrients for bloom development or maintenance. As a generality, in estuaries and enclosed coastal embayments, exogenous nutrients are often necessary for high biomass blooms to be initiated, but due to long-term buildup of nutrients in estuaries, leading to large sediment reserves of nutrients, recycling and regeneration may sustain blooms at higher densities and for longer periods of time than in years past. Reinforcing feedbacks in estuaries can lead to an acceleration and/or maintenance of eutrophic conditions. For example, increased algal productivity may lead to depressed water column oxygen which, in turn, may result in increased recycling of nitrogen and phosphorus by changes in redox potential, or pH (Kemp et al., 2005; Glibert et al., 2011; Gao et al., 2012). These fluxes will then positively reinforce an ecosystems degradation trajectory and may contribute to blooms being sustained for long periods of time.

One such example is the bloom of *Aureocymbra lagunensis* evident in Laguna Madre, Texas, that lasted for approximately 8 years in the 1990s. Intense rains after years of drought led to a sequence of blooms, and benthic regeneration led to sustained suitable ecosystem conditions (e.g., Buskey et al., 2001). Similarly, a bloom of *Synechococcus* was observed in eastern Florida Bay that followed an injection of phosphorus from two apparent sources: high freshwater discharge from Hurricanes Katrina, Rita, and Wilma that impacted south Florida in 2005 and a very high organic loading from a unique situation of road construction that required mulching of significant amounts of mangroves (Madden, 2010). Consequently, chlorophyll concentrations rose and were sustained at levels roughly eightfold higher than pre-bloom levels for up to 18 months, while such an increase in phosphorus concentration was only observed during the initiation stages of the bloom and then declined.

Detection, prediction, mitigation, and control

Rapid advances are being made in the ability to detect HABs and, in some cases, predict their occurrence and potentially reduce their impacts. Rapid detection capabilities have evolved from classic microscopic methods to detection involving specific molecules and genomes. For example, numerous methods have been developed targeting antibodies against cell surface antigens that are specific for a specific HAB or HAB group that can be detected with a fluorescent signal (reviewed by Sellner et al., 2003). Additionally, molecular probes have been developed for many species, targeting the ribosomal RNA genes and/or their transcriptional products. Many taxon-species probes have been developed.

New methods have been advanced for detection of toxins as well, and some are field based. Additionally, much progress has been advanced in the use of remote sensing capabilities, both remote imagery as well as moored packages and arrays that can detect and provide real-time information on species as well as associated chemistry and physical parameters. Such packages include both moored arrays and remotely operated vehicles that can survey areas more efficiently than was possible from classic shipboard approaches (Sellner et al., 2003). A suite of over 50 such probes in the State of Maryland is allowing managers and the public alike to monitor trends in Chesapeake Bay and rapidly respond when conditions warrant (www.eyesonthebay.net). In situ nutrient sensors are also advancing, with capability developing for some organic forms of nutrients as well as inorganic forms, so that relationships between pulses in nutrient delivery and alterations in salinity due to rainfall, for example, are now possible to establish (Glibert et al., 2005b; Glibert et al., 2008).

Models and forecasting of blooms are advancing very rapidly. There are two general types of HAB models that are useful for management applications. The first is the development of models that predict “general likelihood

of occurrence” of HAB species, whereas the second is the development of models that include “explicit” predictions of HAB occurrence in time or space. The former is useful for management in application of long-term actions to reduce the likelihood of future occurrences, i.e., prevention. The latter requires more refinement to understand the physics, biology, and chemistry of the environment, but it can be of more value at the local community level. Coupling the knowledge of the biology of the organisms of interest with robust circulation models of the area of interest has allowed real-time forecasts to be possible. An excellent example of this developing skill is the model that has been developed for *Karenia brevis* blooms off the coast of Florida. This model uses satellite imagery together with a regional circulation model, predicted wind fields, and several biological parameters to forecast where blooms may be found in a several-day period. Operational forecasts are now provided to the public for Florida and several other regions of the United States where similar capabilities are advancing (<http://tidesandcurrents.noaa.gov/hab/>).

Understanding and predicting algal blooms is important, but the ultimate goal is reducing their occurrence or their impacts once they do occur. The most effective strategy for reducing their likelihood is nutrient reduction. The best cited example illustrating the effectiveness of nutrient reduction is from the Seto Inland Sea in Japan. Between 1965 and 1976, the number of “red tide” outbreaks (high biomass blooms) increased sevenfold, in parallel with the increase in industrial production, but in 1973, Japanese authorities instituted the Seto Inland Sea Law to reduce loadings to half of the 1974 levels over a 3-year period. The number of red tides began to decrease in 1977, eventually falling to less than 30 % of the peak frequency, which had been in excess of 300 blooms per year (reviewed by Imai et al., 2006).

Bloom control strategies may also take the form of mechanical control, the use of filters or booms to remove or exclude cells from certain areas and use of chemical compounds to kill or inhibit bloom cells, or biological control, the use of organisms or pathogens that can lyse, kill, or remove the HABs. Some efforts are finding success with the use of clays that flocculate and remove the HAB cells from the area. Use of clays is well advanced in Korean waters where clay application is used to protect fish cages when HABs develop (Kim, 2006). Overall, however, all of these control measures may have uncertain or unknown environmental impacts, and all such approaches are in early stages of research and development.

Summary and conclusions

In sum, while some algal blooms, such as spring blooms, are natural characteristics of many temperate and coastal waters, and critically important for food webs of marine and freshwater ecosystems, HABs are, in large part, a consequence of anthropogenic activities. HABs are increasing in frequency, magnitude, and ecological and

economic effects throughout the world. Understanding of toxins, human health impacts, and the socioeconomic consequences of these blooms – to fisheries and economies – is emerging, but many questions remain unanswered, particularly as new toxins are discovered or characterized. One of the most significant factors contributing to their expansion – particularly in estuaries – is increased nutrient loading from sewage effluent, agriculture, animal operations, and aquaculture. What is clear is that the historic view of phytoplankton responses to eutrophication – increased nutrients promotes increased chlorophyll and high biomass blooms, leading to oxygen deduction and losses in habitat (e.g., Cloern, 2001) – is too simplistic for understanding how HABs respond to the major changes in nutrient loads, forms, and stoichiometry that many systems are now sustaining. Nutrient form and proportion matter and many HABs have physiological mechanisms that enable them to thrive in these environments that are being dramatically altered by human influence. Furthermore, the interplay of biology and physics is only understood at a limited scale, with much to be learned about local scales, microstructures, as well as mesoscale features. Climate changes are adding additional factors that may enhance the likelihood for blooms, and the complexity of ecosystem changes with climate changes means that much is yet to be learned about the direct and indirect effects of climate on HABs. New technologies are advancing toward improved monitoring and prediction, but many such technologies are sophisticated and expensive. Although considerable advances have been made in understanding the biology of HABs, and their interactions with other members of the community at all levels of the food web, there is still much to be learned about how and why specific species respond to specific conditions.

Bibliography

- Adolf, J. E., Bachvaroff, T., and Place, A. R., 2008. Cryptophyte abundance drives blooms of mixotrophic harmful algae: a hypothesis based on *Karlodinium veneficum* as a model system. *Harmful Algae*, **8**, 119–128.
- Alvarez-Salgado, X. A., Figueiras, F. G., Perez, F. F., Groom, S., Nogueira, E., Borges, A., Chou, L., Castro, C. G., Moncoiffe, G., Rios, A. F., Miller, A. E. J., Frankignoulle, M., Savidge, G., and Wollast, R., 2003. The Portugal coastal counter current of NW Spain: new insights on its biogeochemical variability. *Progress in Oceanography*, **56**, 281–321.
- Anderson, D. M., Glibert, P. M., and Burkholder, J. M., 2002. Harmful algal blooms and eutrophication: nutrient sources, composition and consequences. *Estuaries*, **25**, 562–584.
- Azanza, R., and Taylor, M., 2001. Are *Pyrodinium* blooms in the southeast Asian region recurring and spreading? A view at the end of the millennium. *AMBIO: A Journal of the Human Environment*, **30**, 356–364.
- Backer, L. C., and McGillicuddy, D. J., 2006. Harmful algal blooms: at the interface between coastal oceanography and human health. *Oceanography*, **19**(2), 94–106.
- Bargu, S., Goldstein, T., Roberts, K., Li, C., and Gulland, F., 2012. *Pseudo-nitzschia* blooms, domoic acid, and related California sea lion strandings in Monterey Bay, California

- Marine Mammal Science. *Nature Geoscience*, doi:10.1111/j.1748-7692.2011.00480.x.
- Bates, S. S., Douglas, D. J., Doucette, G. J., and Leger, C., 1995. Enhancement of domoic acid production by reintroducing bacteria to axenic cultures of the diatom *Pseudo-nitzschia multiseries*. *Natural Toxins*, **3**, 428–435.
- Beman, J. M., Arrigo, K. R., and Matson, P. A., 2005. Agricultural runoff fuels large phytoplankton blooms in vulnerable areas of the ocean. *Nature*, **434**, 211–214.
- Bouwman, A. F., Pawlowski, M., Liu, C., Beusen, A. H. W., Shumway, S. E., Glibert, P. M., and Overbeek, C., 2011. Global hindcasts and future projections of coastal nitrogen and phosphorus loads due to shellfish and seaweed aquaculture. *Reviews in Fisheries Science*, **19**, 331–357.
- Bouwman, A. F., Beusen, A. H. W., Overbeek, C. C., Bureau, D. P., Pawlowski, M., and Glibert, P. M., 2013. Hindcasts and future projects of global inland and coastal nitrogen and phosphorus loads due to finfish aquaculture. *Reviews in Fisheries Science*, **21**, 112–156.
- Burkholder, J. M., Glibert, P. M., and Skelton, H., 2008. Mixotrophy, a major mode of nutrition for harmful algal species in eutrophic waters. *Harmful Algae*, **8**, 77–93.
- Buskey, E. J., Liu, H., Collumb, C., and Bersano, J. G. F., 2001. The decline and recovery of a persistent Texas brown tide algal bloom in the Laguna Madre (Texas, USA). *Estuaries*, **24**, 337–346.
- Cloern, J. E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series*, **210**, 223–253.
- Davis, T. L., Berry, D. L., Boyer, G. L., and Gobler, C. J., 2009. The effects of temperature and nutrients on the growth and dynamics of toxic and non-toxic strains of *Microcystis* during cyanobacteria blooms. *Harmful Algae*, **8**, 715–7125.
- Diaz, R. J., and Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. *Science*, **321**, 926–928.
- Donaghay, P. L., 1988. The role of temporal scales of acclimation, food quality and trophic dominance in controlling the evolution of copepod feeding behaviour. *Bulletin of Marine Science*, **43**, 469–485.
- Edvardsen, B., and Imai, I., 2006. The ecology of harmful flagellates within Prymnesiophyceae and Raphidophyceae. In Granéli, E., and Turner, J. (eds.), *The Ecology of Harmful Algae*. New York: Springer-Verlag, pp. 67–80.
- Edvardsen, B., and Paasche, E., 1998. Bloom dynamics and physiology of *Prymnesium* and *Chrysochromulina*. In Anderson, D. M., Cembella, A. D., and Hallegraeff, G. M. (eds.), *Physiological Ecology of Harmful Algal Blooms*. Berlin, Germany: Springer-Verlag, pp. 193–208.
- Flynn, K. J., Stoecker, D. K., Mitra, A., Raven, J. A., Glibert, P. M., Hansen, P. J., Granéli, E., and Burkholder, J. M., 2013. Misuse of the phytoplankton-zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *Journal of Plankton Research*, **35**, 3–11.
- Franks, P. J. S., 1992. Sink or swim: accumulation of biomass at fronts. *Marine Ecology Progress Series*, **82**, 1–12.
- Fuhrman, J. A., and Suttle, C. A., 1993. Viruses in marine planktonic systems. *Oceanography*, **6**, 50–62.
- Furuya, K., Glibert, P. M., Zhou, M., and Raine, R. (eds.), 2010. *GEOHAB Asia- Global Ecology and Oceanography of Harmful Algal Blooms in Asia*. Paris, France: IOC and SCOR.
- Gao, Y., Cornwell, J. C., Stoecker, D. K., and Owens, M. S., 2012. Effects of cyanobacterial-driven pH increases on sediment nutrient fluxes and coupled nitrification-denitrification in a shallow fresh water estuary. *Biogeosciences*, **9**, 2697–2710.
- Gentien, P., Reguera, B., Yamazaki, H., Femand, L., Berdalet, E., and Raine, R. (eds.), 2008. *GEOHAB Core Research Project: HABs in Stratified Systems*. Paris, France: IOC and SCOR.
- Gisselson, L.-Å., Carlsson, P., Granéli, E., and Pallon, J., 2002. *Dinophysis* blooms in the deep euphotic zone of the Baltic Sea: do they grow in the dark? *Harmful Algae*, **1**, 401–418.
- Glibert, P. M., and Burkholder, J. M., 2006. The complex relationships between increasing fertilization of the earth, coastal eutrophication, and HAB proliferation. In Granéli, E., and Turner, J. (eds.), *The Ecology of Harmful Algae*. New York: Springer-Verlag, pp. 341–354.
- Glibert, P. M., and Burkholder, J. M., 2011. Eutrophication and HABs: strategies for nutrient uptake and growth outside the Redfield comfort zone. *Chinese Journal of Oceanology and Limnology*, **29**, 724–738.
- Glibert, P. M., and Legrand, C., 2006. The diverse nutrient strategies of HABs: focus on osmotrophy. In Granéli, E., and Turner, J. (eds.), *The Ecology of Harmful Algae*. New York: Springer-Verlag, pp. 163–176.
- Glibert, P., and Pitcher, G. (eds.), 2001. *GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms Programme) Science Plan*. Baltimore, MA: SCOR and IOC.
- Glibert, P. M., Magnien, R., Lomas, M. W., Alexander, J., Fan, C., Haramoto, E., Trice, T. M., and Kana, T. M., 2001. Harmful algal blooms in the Chesapeake and Coastal Bays of Maryland, USA: comparisons of 1997, 1998, and 1999 events. *Estuaries*, **24**, 875–883.
- Glibert, P. M., Anderson, D. A., Gentien, P., Granéli, E., and Sellner, K. G., 2005a. The global, complex phenomena of harmful algal blooms. *Oceanography*, **18**(2), 136–147.
- Glibert, P. M., Seitzinger, S., Heil, C. A., Burkholder, J. M., Parrow, M. W., Codispoti, L. A., and Kelly, V., 2005b. The role of eutrophication in the global proliferation of harmful algal blooms: new perspectives and new approaches. *Oceanography*, **18**, 198–209.
- Glibert, P. M., Mayorga, E., and Seitzinger, S., 2008. *Prorocentrum minimum* tracks anthropogenic nitrogen and phosphorus inputs on a global basis: application of spatially explicit nutrient export models. *Harmful Algae*, **8**, 33–38.
- Glibert, P. M., Allen, J. I., Bouwman, L., Brown, C., Flynn, K. J., Lewitus, A., and Madden, C., 2010. Modeling of HABs and eutrophication: status, advances, challenges. *Journal of Marine Systems*, **83**, 262–275.
- Glibert, P. M., Fullerton, D., Burkholder, J. M., Cornwell, J., and Kana, T. M., 2011. Ecological stoichiometry, biogeochemical cycling, invasive species and aquatic food webs: San Francisco Estuary and comparative systems. *Reviews in Fisheries Science*, **19**, 358–417.
- Glibert, P. M., Burkholder, J. M., and Kana, T. M., 2012. Recent advances in understanding of relationships between nutrient availability, forms and stoichiometry and the biogeographical distribution, ecophysiology, and food web effects of pelagic and benthic *Prorocentrum* spp. *Harmful Algae*, **14**, 231–259.
- Gobler, C. J., and Sañudo-Wilhelmy, S. A., 2001. Temporal variability of groundwater seepage and brown tide blooms in a Long Island embayment. *Marine Ecology Progress Series*, **217**, 299–309.
- Granéli, E., and Flynn, K., 2006. Chemical and physical factors influencing toxin content. In Granéli, E., and Turner, J. (eds.), *The Ecology of Harmful Algae*. New York: Springer-Verlag, pp. 229–241.
- Granéli, E., and Johansson, N., 2003. Increase in the production of allelopathic substances by *Prymnesium parvum* cells grown under N- or P-deficient conditions. *Harmful Algae*, **2**, 135–145.
- Granéli, E., Edler, L., Gedziorowska, D., and Nyman, U., 1985. Influence of humic and fulvic acids on *Prorocentrum minimum* (Pav.) Schiller. In Anderson, D. M., White, A. W., and Baden, D. G. (eds.), *Toxic Dinoflagellates*. New York: Elsevier, pp. 201–206.

- Granéli, E., Carlsson, P., and Legrand, C., 1999. The role of C, N and P in dissolved and particulate matter as a nutritional source for phytoplankton growth, including toxic species. *Aquatic Ecology*, **33**, 17–27.
- Harrison, P. J., Furuya, K., Glibert, P. M., Xu, J., Liu, H. B., Yin, K., Lee, J. H. W., Anderson, D. M., Gowen, R., Al-Azri, A. R., and Ho, A. Y. T., 2011. Geographical distribution of red and green *Noctiluca scintillans*. *Chinese Journal of Oceanology and Limnology*, **29**, 807–831.
- Heil, C. A., Glibert, P. M., and Fan, C., 2005. *Prorocentrum minimum* (Pavillard) Schiller: a review of a harmful algal bloom species of growing worldwide importance. *Harmful Algae*, **4**, 449–470.
- Heisler, J., Glibert, P. M., Burkholder, J. M., Anderson, D. A., Cochlan, W. P., Dennison, W. C., Dortch, Q., Gobler, C., Heil, C. A., Humphries, E., Lewitus, A., Magnien, R., Marshall, H., Sellner, K., Stockwell, D., Stoecker, D., and Suddleson, M., 2008. Eutrophication and harmful algal blooms: a scientific consensus. *Harmful Algae*, **8**, 3–13.
- Howarth, R. W., 2008. Coastal nitrogen pollution: a review of sources and trends globally and regionally. *Harmful Algae*, **8**, 14–20.
- Hu, C., Li, D., Chen, C., Ge, J., and Muller-Karger, F. E., 2010. On the recurrent *Ulva prolifera* blooms in the Yellow Sea and East China Sea. *Journal of Geophysical Research*, **115**(C05017), 2.
- Ibelings, B. W., and Chorus, I., 2007. Accumulation of cyanobacterial toxins in freshwater “seafood” and its consequences for public health: a review. *Environmental Pollution*, **150**, 177–192.
- Imai, I., Yamaguchi, M., and Hori, Y., 2006. Eutrophication and occurrences of harmful algal blooms in the Seto Inland Sea, Japan. *Plankton and Benthos Research*, **1**, 71–84.
- Johnson, P., Townsend, A., Cleveland, C. C., Glibert, P. M., Howarth, R., Mackenzie, V., Rejmankova, E., and Ward, M., 2010. Linking environmental nutrient enrichment and disease emergence in humans and wildlife. *Ecological Applications*, **20**, 16–29.
- Kamykowski, D., Yamazaki, H., Yamazaki, A. K., and Kirkpatrick, G. J., 1998. A comparison of how different orientation behaviors influence dinoflagellate trajectories and photoresponses in turbulent water columns. In Anderson, D. M., Cembella, A. D., and Hallegraeff, G. M. (eds.), *Physiological Ecology of Harmful Algal Blooms*. Berlin, Germany: Springer-Verlag, pp. 581–599.
- Kemp, W. M., Boynton, W. R., Adolf, J. E., Boesch, D. F., Boicourt, W. C., Brush, G., Cornwell, J. C., Fisher, T. R., Glibert, P. M., Hagy, J. D., Harding, L. W., Houde, E. D., Kimmel, D. G., Miller, W. D., Newell, R. I. E., Roman, M. R., Smith, E. M., and Stevenson, J. C., 2005. Eutrophication in Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series*, **303**, 1–29.
- Kim, H. G., 2006. Mitigation and control of HABs. In Granéli, E., and Turner, J. (eds.), *The Ecology of Harmful Algae*. New York: Springer-Verlag, pp. 327–340.
- Lancelot, C., 1995. The mucilage phenomenon in the continental coastal waters of the North Sea. *Science of the Total Environment*, **165**, 83–102.
- Lancelot, C., Martin, J. M., Panin, N., and Zaitsev, Y., 2002. The North-western Black Sea: a pilot site to understand the complex interaction between human activities and the coastal environment. *Estuarine, Coastal and Shelf Science*, **54**, 279–283.
- Landsberg, J., 2002. The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science*, **10**, 113–190.
- Madden, C., 2010. Case study: Florida Bay. In Glibert, P. M., Madden, C., Boynton, W., Flemer, D., Heil, C., and Sharp, J. (eds.), *Nutrients in Estuaries. A Summary Report of the National Estuarine Experts Workgroup, 2006–2007*. EPA Office of Water. <http://water.epa.gov/scitech/swguidance/standards/criteria/nutrients/upload/Nutrients-in-Estuaries-November-2010.pdf>
- Mitra, A., and Flynn, K. J., 2010. Modelling mixotrophy; more or less the sum of the parts? *Journal of Marine Systems*, **83**, 158–169.
- Moore, S. K., Trainer, V. L., Mantua, N. J., Parker, M. S., Laws, E. A., Backer, L. C., and Flemming, L. E., 2008. Impacts of climate variability and future change on harmful algal blooms and human health. *Environmental Health*, **7**, S4, doi:10.1186/1476-069X-7-S2-S4.
- O’Neil, J. M., Davis, T. W., Burford, M. A., and Gobler, C. J., 2012. The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change. *Harmful Algae*, **14**, 313–334.
- Paerl, H. W., and Millie, D. F., 1996. Physiological ecology of toxic aquatic cyanobacteria. *Phycologia*, **35**(Suppl. 6), 160–167.
- Parsons, M. L., Dortch, Q., and Turner, R. E., 2002. Sedimentological evidence of an increase in *Pseudo-nitzschia* (Bacillariophyceae) abundance in response to coastal eutrophication. *Limnology and Oceanography*, **47**, 551–558.
- Roeke, D. L., Errera, R. M., Kiesling, R., Brooks, B. W., Grover, J. P., Schwierzke, L., Ureña-Boeck, F., Baker, J., and Pinckney, J. L., 2007. Effects of nutrient enrichment on *Prymnesium parvum* population dynamics and toxicity: results from field experiments, Lake Possum Kingdom, USA. *Aquatic Microbial Ecology*, **46**, 125–140.
- Scholin, C. A., Gulland, F., Doucette, G. J., Bensen, S., Busman, M., Chavez, F. P., Cordaro, J., DeLong, R., DeVogelaere, A., Harvey, J., Haulena, M., Lefebvre, K., Lipscomb, T., Loscutoff, S., Lowenstine, L. J., Marin, R., III, Miller, P. E., McLellan, W. A., Moeller, P. D. R., Powell, C. L., Rowles, T., Silvagni, P., Silber, M., Spraker, T., Trainer, V. L., and Van Dolah, F. M., 2000. Mortality of sea lions along the central California coast linked to a toxic diatom bloom. *Nature*, **403**, 80–84.
- Sellner, K. G., Doucette, G. J., and Kirkpatrick, G. J., 2003. Harmful algal blooms: causes, impacts and detection. *Journal of Industrial Microbiology and Biotechnology*, **3**, 383–406.
- Smayda, T. J., 2002. Adaptive ecology, growth strategies and the global bloom expansion of dinoflagellates. *Journal of Oceanography*, **58**, 281–294.
- Sunda, W. G., Granéli, E., and Gobler, C. J., 2006. Positive feedback and the development and persistence of ecosystem disruptive algal blooms. *Journal of Phycology*, **42**, 963–974.
- Tracey, G. A., 1988. Feeding reduction, reproductive failure, and mortality in *Mytilus edulis* during the 1985 “brown tide” in Narragansett Bay, Rhode Island. *Marine Ecology Progress Series*, **50**, 73–81.
- Trainer, V. L., Le Eberhart, B.-T., Wekell, J. C., Adams, N. G., Hanson, L., Cox, F., and Dowell, J., 2003. Paralytic shellfish toxins in Puget Sound, Washington. *Journal of Shellfish Research*, **22**, 213–223.
- Trainer, V. L., Cochlan, W. P., Erickson, A., Bill, B. D., Cox, F. H., Borchert, J. A., and Lefebvre, K. A., 2007. Recent domoic acid closures of shellfish harvest areas in Washington State inland waterways. *Harmful Algae*, **6**, 449–459.
- Trainer, V. L., Bates, S. S., Lundholm, N., Thessen, A. E., Cochlan, W. P., Adams, N. C., and Trick, C. G., 2012. *Pseudo-nitzschia* physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health. *Harmful Algae*, **14**, 271–300.

Cross-references

Ecological Stoichiometry
Eutrophication



<http://www.springer.com/978-94-017-8800-7>

Encyclopedia of Estuaries

Kennish, M.J. (Ed.)

2016, XXIX, 760 p. 330 illus., 197 illus. in color.,

Hardcover

ISBN: 978-94-017-8800-7